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Commercially important species associated with horse mussel (*Modiolus modiolus*) biogenic reefs: a habitat for biodiversity conservation and fisheries benefits

Flora E. A. Kent¹, James M. Mair¹, Jason Newton², Charles Lindenbaum³, Joanne S. Porter¹, William G. Sanderson^{1, 4}

¹*School of Life Sciences, Heriot-Watt University, Edinburgh EH14 4AS, UK*

²*NERC Life Sciences Mass Spectrometry Facility, Scottish Universities Environmental Research Centre, Rankine Avenue, East Kilbride G75 0QF, UK*

³*Natural Resources Wales, Maes y Ffynnon, Bangor, Gwynedd LL57 2DW*

⁴*St Abbs Marine Station, St Abbs, Scottish Borders, TD14 5PW*

Highlights

- Communities of conspicuous megafauna were assessed on *Modiolus modiolus* reefs, sand and cobble habitats.
- Tissue samples from reef fauna were subject to stable isotope analysis to investigate trophic structure.
- *M. modiolus* reefs support a higher abundance of commercially important shellfish, including *Aequipecten opercularis*, *Buccinum undatum* and *Maja brachydactyla*, than cobble and sand habitats.
- Evidence of the commercial value of *M. modiolus* reefs in the UK.

Abstract

Horse mussel beds (*Modiolus modiolus*) are protected biodiversity hotspots in Marine Protected Areas of the NE Atlantic. In this study, horse mussel beds, cobble habitats and sandy habitats were assessed using underwater visual census and drop-down video techniques in three UK regions. Megafauna were enumerated, differences in community composition and individual species abundances were analysed. Samples of conspicuous megafauna were also collected from horse mussel beds in Orkney for stable isotope analysis.

Communities of conspicuous megafauna were different between horse mussel habitats and other habitats throughout their range. Three commercially important species: whelks (*Buccinum undatum*), queen scallops (*Aequipecten opercularis*) and spider crabs (*Maja*

brachydactyla) were significantly more abundant (by as much as 20 times) on horse mussel beds than elsewhere. Isotopic analysis provided insights into their trophic relationship with the horse mussel bed. Protection of *M. modiolus* habitat can achieve biodiversity conservation objectives whilst benefiting fisheries also.

Introduction

Globally, fish stocks are under threat (Jackson et al., 2001) with the proportion of over-exploited fish stocks at 32% in 2008 (FAO, 2010), leading to calls to halt this trend and restore them (Worm et al., 2009). One method of improving fisheries management has been a shift to ‘Ecosystem-Based Management’ (EBM) that involves a move from traditional single species based management to a greater understanding of the interactions between habitats and commercially important species. In the NE Atlantic, habitat-forming species such as maerl (a coralline red algae) create a physically complex and biodiverse seabed, which provides a nursery ground for commercially important fish and shellfish (Kamenos et al., 2004a, 2004b). *Modiolus modiolus* (horse mussel) reefs are structurally complex habitats, characterised by high species diversity (Hirst et al., 2012; Rees et al., 2008; Sanderson et al., 2008). The societal benefits of horse mussel reefs for fishermen has been demonstrated (Kent et al 2016); yet the utilisation of horse mussel reefs as a resource for benthic consumers has not been studied.

In the United States, the Sustainable Fisheries Act (SFA) now requires fisheries managers to identify the ‘Essential Fish Habitat’ (EFH) for commercially important fish species (Fluharty, 2000), i.e. “those waters and substrate necessary to fish spawning, feeding or growth to maturity” (NOAA, 1966). This concept is not confined to describing finfish habitat associations; it has also been used for invertebrates such as conch (Glazer and Kidney, 2004), octopus (Garofalo et al., 2011) and even bottlenose dolphin (Ingram and Rogan, 2002).

The EBM approach extends the focus of managing resources beyond the target species and includes impacts to non-target species and benthic habitats, supporting ecological processes that are required to sustain harvestable resources (Hughes et al., 2005). With an increasing human population comes an increased demand for ecosystem goods and services, i.e. “the benefits natural ecosystems provide to human society” (de Groot et al., 2002). In the marine

environment, there is increasing interest in the relationship between biodiversity and ecosystem services given the wide scale loss of biodiversity in marine ecosystems (Worm et al., 2006). Marine Protected Areas (MPAs) are seen as an important management tool to conserve species and habitats (Tundi Agardy, 1994) and, over time, well managed MPAs can support ecosystem services to provide ecological and societal benefits (Fox et al., 2012).

Those implementing the Habitats Directive across Europe have rarely evaluated the ecosystem services or the commercial value of the biodiversity that they seek to maintain (Maes et al., 2012). Marine biodiversity conservation is lagging behind the terrestrial equivalent, and increasing uses and demands on the marine environment have led to the development of policy frameworks that integrate human activities as part of the system (Atkins et al., 2011). Historically, biodiversity management and fisheries management have been developed separately due to constraints imposed on sectors and fundamentally different aspirations. Thus, the motivation to identify EFH is not provided through fisheries legislation in Europe or spatial management of marine habitats either. However, recognition of habitat associations and appropriate management of EFH has the potential to provide benefits for both fisheries and nature conservation.

Identifying a habitat as an EFH is not a simple task, especially for highly mobile species that use a range of habitats throughout their life cycle. With limited resources, conserving or restoring every habitat used by a fish is unrealistic, therefore identifying habitats that are used during sensitive life stages are often prioritised (Levin and Stunz, 2005). Relative fish abundance measurements provide an initial insight into which areas are important for fish and shellfish. However, to recognise a habitat as an EFH requires a greater understanding of the functional role of the habitat, i.e. whether it is being used for feeding or reproduction, etc.

Stable isotope analysis is becoming a popular method for studying food webs (Schaal et al., 2012). ^{15}N becomes enriched during trophic transfers, with a mean increase (or “trophic enrichment factor”, TEF) of 3.4‰ (Minagawa and Wada, 1984; Post, 2002) equivalent to approximately one trophic level, though there are variations, with TEF being larger for herbivorous fish (Mill et al., 2007). The $\delta^{13}\text{C}$ from the tissue of an animal is more conservative with trophic transfer, instead reflecting the source(s) of

carbon in the food chain. Analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ together can be used to determine the feeding relationships on a biogenic habitat (Grall et al., 2006), benthic-pelagic coupling (McIntyre et al., 2006) and habitat associations (Yeager and Layman, 2011).

UK biogenic reefs have been recognised as biodiversity hotspots, e.g. *M. modiolus* reefs; (Mair et al., 2000; Moore et al., 2013; Rees, 2009) and mapped for conservation purposes, e.g. Lindenbaum et al. (2008). However, our understanding of habitat associations and the trophic structure of many biogenic reef communities is limited. Underwater Visual Censuses (UVCs) can be used to measure relative megafauna abundance (Kamenos et al., 2004b) and the benefit of using this technique is that it is non-destructive and independent of fishing gear bias. Remotely Operated Vehicles (ROVs) and towed videos have also been used to record the abundance of mobile species associated with coral reefs (Söffker et al., 2011) and gorgonians (De Clippele et al., 2015).

As structurally complex seabed features, *M. modiolus* reefs are expected to provide a 'habitat provision' ecosystem service that has been shown to be the case for other biogenic structures (De Clippele et al., 2015; Kamenos et al., 2004b; Margiotta et al., 2016). However, *M. modiolus* reefs are relatively inaccessible and their ecological function is understudied. The aim of this study is to identify the key megafaunal species (defined as animals greater than 2 cm maximum length) associated with three *M. modiolus* reefs in the UK and to investigate the trophic feeding niche structure of a *M. modiolus* reef megafaunal community.

Methods

Megafauna abundance

Underwater Visual Censuses (UVCs) were carried out using SCUBA at twenty-three sites in Shetland and Orkney (Figure 1 B and C) between 15 and 25 m below chart datum. It was impractical to survey at multiple sites at Pen Llŷn (Figure 2 D) due to strong currents and short slack water periods, therefore a Drop Down Video (DDV) camera system was used. Sites in Orkney and Shetland were surveyed in May 2013 and September 2012 respectively. Sites off Pen Llŷn were surveyed between May and June of 2008 and 2010. In all cases, conspicuous megafauna, including fish and commercially important invertebrates such as shellfish, were quantified.

UVC sites were selected at random using extant video footage and preliminary dive data to stratify sampling to ‘horse mussel reef’ (8 sites), ‘sand’ (8 sites) or ‘cobble’ (7 sites) habitats. Horse mussel reef sites had a density of > 20 *M. modiolus* m⁻². All observers were trained in species identification during a pilot study in May 2012 in Orkney and all surveys covered a 60 m² area delineated by a transect tape deployed from a shot-line. Habitats were verified as cobble, sand or *M. modiolus* reef using photoquadrats and granulometry samples.

The DDV camera system used was a Sony Model DCR-TRV950 camcorder fitted into a tubular aluminium housing with two HID video lamps and lasers (10cm apart) were used to quantify the seabed area covered. The video surface unit included a labelling system that overlaid GPS position and depth information onto the surface image for recording and viewing. DDV camera tows were approximately 100 m in length, but actual distances were calculated from the GPS start and end points and a section of 4-8 minutes was edited from the video clip for analysis. Video footage that was too fast (>30 m per minute) or with less than 1 m visibility was disregarded. Eight *M. modiolus* reef sites were sampled off Pen Llŷn as well as 8 cobble sites and 8 sand sites.

Food web analysis

Thirty-seven samples were collected for stable isotope analysis from eleven species across three *M. modiolus* reef sites in Orkney (see Supplementary Table S1 for sampling locations) from the 1st-5th December 2013. *Aequipecten opercularis* (n=6), *Leocarcinus depurator* (n=5), *Asterias rubens* (n=1) and *Buccinum undatum* (n=5) were collected using SCUBA by searching the reef from a central location or on a drift dive. *M. modiolus* (n=14) and polychaetes (n=3) were collected using a ‘clump sample’ technique where a clump of 3-5 *M. modiolus* and associated fauna are placed into a bucket along with the underlying sediment (Mair et al., 2000). *Gadus morhua* (n=1) and *Taurulus bubalis* (n=3) were collected from sites adjacent to the reefs using baited creels.

White muscle was taken from the fish samples and adductor from the bivalves, while the foot muscle was dissected from the *B. undatum* samples. Gill tissue was taken from the crustaceans and tube feet from *A. rubens*. Samples were freeze-dried and ground to a fine powder using a pestle and mortar. Approximately 1 mg of tissue from each sample was loaded into a 4 x 6 mm tin capsule and combusted in continuous flow isotope ratio mass

spectrometer (CF-IRMS). Results are expressed as parts per thousand (‰) deviations from international standards, in delta (δ) notation.

Data Analysis

Megafauna counts from the Underwater Visual Censuses (UVCs) and those from the Drop Down Video (DDV) transects were analysed separately due to the different methodology used. For the multivariate analysis, all data were log transformed to down-weight very abundant species (e.g. *Echinus esculentus* abundance varied by three orders of magnitude). Using Bray-Curtis similarity, Analysis of Similarities (ANOSIM) (Clarke and Gorley, 2006) was used to test for differences in megafaunal communities between *M. modiolus* reef, sand and cobble habitats.

A SIMPER analysis was used to examine the key species driving the differences in community composition (Clarke and Gorley, 2006). Counts of the three species contributing the most to the difference in megafauna communities at the reef, cobble and sand sites were then analysed using a Kruskal-Wallis test with 'habitat type' as the independent variable. Pairwise Kruskal-Wallis tests were then performed using a chi-squared probability distribution with a Bonferroni correction for multiple comparisons. The stable isotope samples were checked to ensure protein had been analysed: samples with a Carbon/Nitrogen ratio of greater than four were removed as this implies a high lipid content or carbonate in the sample. Samples were averaged for each species where possible and standard deviations calculated. All univariate analyses were carried out in R version 2.9.1 (R Core Development Team, 2011).

Results

Megafauna community analysis

Fifteen megafauna species were recorded from 23 UVC samples in Orkney and Shetland. An ANOSIM shows that the megafaunal community was significantly different amongst habitats ($r = 0.45$, $p = <0.001$). Pairwise tests showed that the megafauna counted at the *M. modiolus* reefs were significantly different to those living on the sand habitats ($r = 0.45$, $p=0.003$) and the cobble habitats ($r = 0.38$, $p = 0.002$). The SIMPER analysis showed that the highest within-group similarity was in the *M. modiolus* reef group (72.68%). The sand habitats were the least similar group, with an average similarity of 19.59%. The high counts of flatfish and

dragonets at sand sites contributed 70% of the similarity within the sandy sites. *M. modiolus* reef sites were most dissimilar to the sand sites (90.41% dissimilarity) and 50% of this dissimilarity was attributable to higher densities of *E. esculentus*, *A. opercularis* and *B. undatum* on the reefs sites (SIMPER; Figure 3a, b and c).

M. modiolus reef sites had over five times more *A. opercularis* than the cobble sites ($\chi^2 = 11.011$, $p=0.001$) and more than 20 times as many as the sand sites ($\chi^2 = 12.427$, $p<0.001$). *B. undatum* were almost twenty times more abundant on reef sites compared to sand sites ($\chi^2 = 7.136$, $p=0.008$). However, the counts at the reef sites were not significantly different to the cobble sites at the 0.05 significance level ($\chi^2 = 3.84$, $p=0.050$). The most abundant species found on the *M. modiolus* reefs was *E. esculentus* (0.46 m^{-2}), which was significantly greater than the cobble sites ($\chi^2 = 9.442$, $p=0.002$) and the sand sites ($\chi^2 = 12.308$, $p<0.001$).

On the UVC transects, gobies (*Pomatoschistus pictus* and *Pomatoschistus microps*) were abundant in all habitats, but especially the sand sites (a maximum of 24 *P. pictus* counted on one transect). Juvenile flatfish (*Limanda limanda*) were abundant at two of the sand sites and dragonets (*Callionymus spp*) were present at three out of eight sand sites (16 counted in total). The fish species associated with the *M. modiolus* sites were almost entirely different to those associated with the sand sites (with the exception of *Callionymus sp.* and *Pomatoschistus pictus*, which occurred in both habitats). The cling-fish *Diplecogaster bimaculata* occurred at the *M. modiolus* sites but not at the off-reef sites.

A total of 22 species were identified from the DDV analysis at 23 sites off the Pen Llyn. The megafaunal community associated with the *M. modiolus* reef was significantly different to the sand and cobble habitats (ANOSIM, $r=0.26$, $p<0.001$). The top three species highlighted in the SIMPER analysis, contributing to the difference in community structure between *M. modiolus* reef sites and off-reef sites, were *B. undatum*, *A. rubens* and *Maja brachydactyla* (previously known as *Maja squinado*: Sotelo et al., 2007). The cumulative contribution of these three species in the difference between habitats was 44.15% between reef and sand habitats, and 44.72% between reef and cobble habitats. Other key species causing differences in the species assemblages were curled octopus (*Eledone cirrhosa*) and butterfish (*Pholis gunnelus*), which were only seen at *M. modiolus* reef sites.

The DDV transects showed that *A. rubens* was the most abundant conspicuous megafaunal species and there were significantly more observed on the reef than the sand ($x^2 = 9.26$, $p < 0.001$) and cobble habitats ($x^2 = 11.618$, $p = 0.002$). *B. undatum* were rarely seen on the DDV surveys compared to the UVCs (0.01 m^{-2} compared to 0.11 m^{-2} respectively). From the DDV analysis, no *B. undatum* were observed on cobble sites, although they were occasionally seen on the reef (0.02 m^{-2}) and sand sites (0.01 m^{-2}). Ballan wrasse (*Labrus bergylta*) occurred on the cobble sites but not on the sand sites. Sea scorpions (*Taurulus bubalis*) occurred at the reef sites and the cobble sites but not on the sandy sites, whereas dogfish (*Scyliorhinus canicula*) occurred on the reef sites and the sand sites but not the cobble sites.

Foodweb analysis

The *M. modiolus*, *A. opercularis*, and *B. undatum* samples from Orkney showed consistent stable isotope signatures (Figure 4). Even *M. modiolus* samples from different reefs (up to 2km apart) showed very similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. For the megafauna tissue samples analysed, $\delta^{15}\text{N}$ increases in the following order: *A. opercularis*; *M. modiolus*; *B. undatum* and *Liocarcinus depurator*; *T. bubalis* and *G. morhua*. The average $\delta^{15}\text{N}$ for *M. modiolus* is 9.21‰ compared with 11.56‰ for *B. undatum*. The highest $\delta^{15}\text{N}$ values were from the fish samples, showing that these animals are at the top of the food chain in this study, and possibly feeding on crustaceans and bivalves on the reef. The isotope ratios from *M. modiolus* and *A. opercularis* samples formed two distinct groups with the $\delta^{15}\text{N}$ of *M. modiolus* approximately 2‰ higher than *A. opercularis* (Figure 4).

Discussion

Through *in situ* observations, this study provides evidence that *M. modiolus* reefs across the UK support a high abundance of megafaunal species compared to other habitats, including the commercially valuable shellfish, *A. opercularis*, *B. undatum* and *Maja brachydactyla*. These findings are in keeping with other biodiversity hotspots in the UK, such as maerl beds that provide an important habitat for *A. opercularis*, *A. rubens* and *E. esculentus* (Kamenos et al., 2004b). Structurally complex marine habitats such as oyster beds and seagrass beds also provide a disproportionately important refuge for other species (Bertelli and Unsworth, 2014; Shervette and Gelwick, 2008). However this is the first time that *M. modiolus* reefs have been shown to provide a comparable functional role to these other complex habitats.

The stable isotope data also show the range of feeding mechanisms used within the reef community and the different food sources on the reef available for mobile species. This also gives an insight into the ecological function of the *M. modiolus* reefs and for example, shows that *B. undatum* and *L. depurator* are approximately one trophic level higher than *M. modiolus*. When considered in combination with the high abundance of *B. undatum* relative to other ‘off-reef’ habitats, this suggests that *B. undatum* may be feeding on *M. modiolus*. Although normally considered a scavenger, predation on bivalves by *B. undatum* has been observed in a laboratory setting (Scolding et al., 2007). Habitat heterogeneity is often important for mobile species during different life stages (Kimirei et al., 2011) and *M. modiolus* reef habitats provide a range of physical conditions from fine sediment to large shell gravel and epifauna (Nic Aonghua et al., 2001).

The two survey methods used in this study (UVCs and DDV) together provide a comprehensive method for measuring conspicuous megafauna abundance; a wide range of species were sampled and the area of seabed sampled was easily defined. However, it is likely that cryptic fish species are under-represented in these more complex reef habitats, as indicated by Bozec et al. (2011), and the use of different sampling techniques may be required to fully grasp the different fish species associated with *M. modiolus*. Similarly, the high counts of *B. undatum* on *M. modiolus* reefs in Orkney and Shetland were not mirrored in the DDV transects off Pen Llŷn probably because this is a slow moving semi-cryptic species, which is difficult to identify from DDV footage. Divers on the UVC transects were able to look around objects and check if shellfish were live or dead, which was not possible on the DDV transects. In a parallel study, comparatively high catch rates of *B. undatum* on *M. modiolus* reefs off Pen Llŷn using baited traps (Kent et al., In Review) corroborates the view that DDV is not the best technique for recording this species.

Spider crabs (*Maja brachydactyla*) were highly abundant on the Pen Llŷn *M. modiolus* reef compared to the off-reef sites and this species is harvested throughout Europe, especially in the English Channel and the Mediterranean (Fahy, 2001). Within the UK, *M. brachydactyla* is largely distributed on the south coast of England and Wales; hence the lack of observations on the Orkney and Shetland reef sites, although its distribution may extend further north with rising seawater temperatures (Goodwin et al., 2013). *M. modiolus* reefs often form a mosaic with other biogenic habitat (e.g. maerl in Shetland; Hirst et al., 2013) and it is likely that

mobile species benefit from this variety (Buhl-Mortensen et al., 2010). Further investigations into the diet of the key mobile species identified in this study through stomach content analysis and a more comprehensive stable isotope study would develop understanding of the predator-prey interactions occurring within and between biogenic habitats.

The Underwater Visual Censuses showed very high densities of *A. operculum* on the *M. modiolus* reefs. Elsewhere, juvenile *A. opercularis* has been shown to attach to hard substrates and use rugose structures such as maerl, which provide a refuge from predators (Kamenos et al., 2004c). It is likely that *A. opercularis* utilise *M. modiolus* shell crevices and associated epibiota (Figure 2) to avoid predation and increase post-recruitment survival. Juvenile *A. opercularis* are able to swim, providing the option to move to a more favourable environment once settled, if a different habitat is required.

The present study shows that the two filter feeding species *M. modiolus* and *A. opercularis* fill different trophic niches, which is consistent with Yakovis et al. (2012) who found that horse mussels and ascidians growing together have distinct diets and there is no overlap in the origin of their food. Increasing evidence for differential particle selection in bivalves (Kiorboe and Mohlenberg, 1981; Shumway et al., 1985; Ward and Shumway, 2004) provides a possible explanation for how the filter feeding *M. modiolus* and *A. opercularis* can co-occur in high densities together as adults in a reef environment.

Overall, the high abundance of *A. opercularis*, *B. undatum* and *M. brachydactyla* on reefs in combination with the trophic structure of the former two (Figure 5), provides strong evidence that *M. modiolus* reefs are 'Essential Fish Habitats' for these species. This highlights the value of horse mussel reefs in providing disproportionately more ecosystem services and corresponding benefits to society than other habitats. However, *M. modiolus* reefs along with other shellfish habitats have declined over the past 100 years (Thurstan et al., 2013) and are vulnerable to physical impacts (Cook et al., 2013). Strangford Lough is a Marine Protected Area that was once home to the UK's largest *M. modiolus* reefs ($> 10\text{km}^2$), and the *A. opercularis* trawl fishery boomed there in the 1980s (Strain et al., 2012) causing long-term declines in *M. modiolus* and associated megafauna, with little sign of recovery of this long-lived reef forming species (Elsäßer et al., 2013; Fariñas-Franco and Roberts, 2014). Ironically, therefore, the fisheries benefits that *M. modiolus* reefs can deliver to society can lead to their demise. Indeed, given that many coastal habitats provide important functional

roles for commercially important fish (e.g. nursery, spawning and feeding grounds), it is unsurprising that destruction results in the consequential decline in associated fish landings (see Seitz et al., 2014).

In many countries, including the UK, biodiversity conservation and fisheries management have historically been the responsibility of separate government departments or agencies. However, marine conservation management has progressed from imposed, command-and-control ‘fortress conservation’ approaches to systems that increasingly combine both ‘top-down’ and ‘bottom-up’ governance (Jones, 2014; Kelleher, 1993). Indeed, these more balanced approaches are reflected globally, where the Convention on Biological Diversity Aichi 6 arguably brings biodiversity concerns closer to fisheries management and UN Sustainable Development Goals than ever before. Understanding the ecological interaction between habitats and mobile species is required for the identification of EFH in contemporary sustainable fisheries management. Here we present evidence to illustrate that this concept can be usefully implemented in the context of Marine Spatial Planning to prioritise the most valuable areas of the seabed (Crowder and Norse, 2008). Thus, the protection of fragile habitats of biodiversity importance can intersect with sustainable fisheries to achieve ecosystem-based management.

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543 Figures

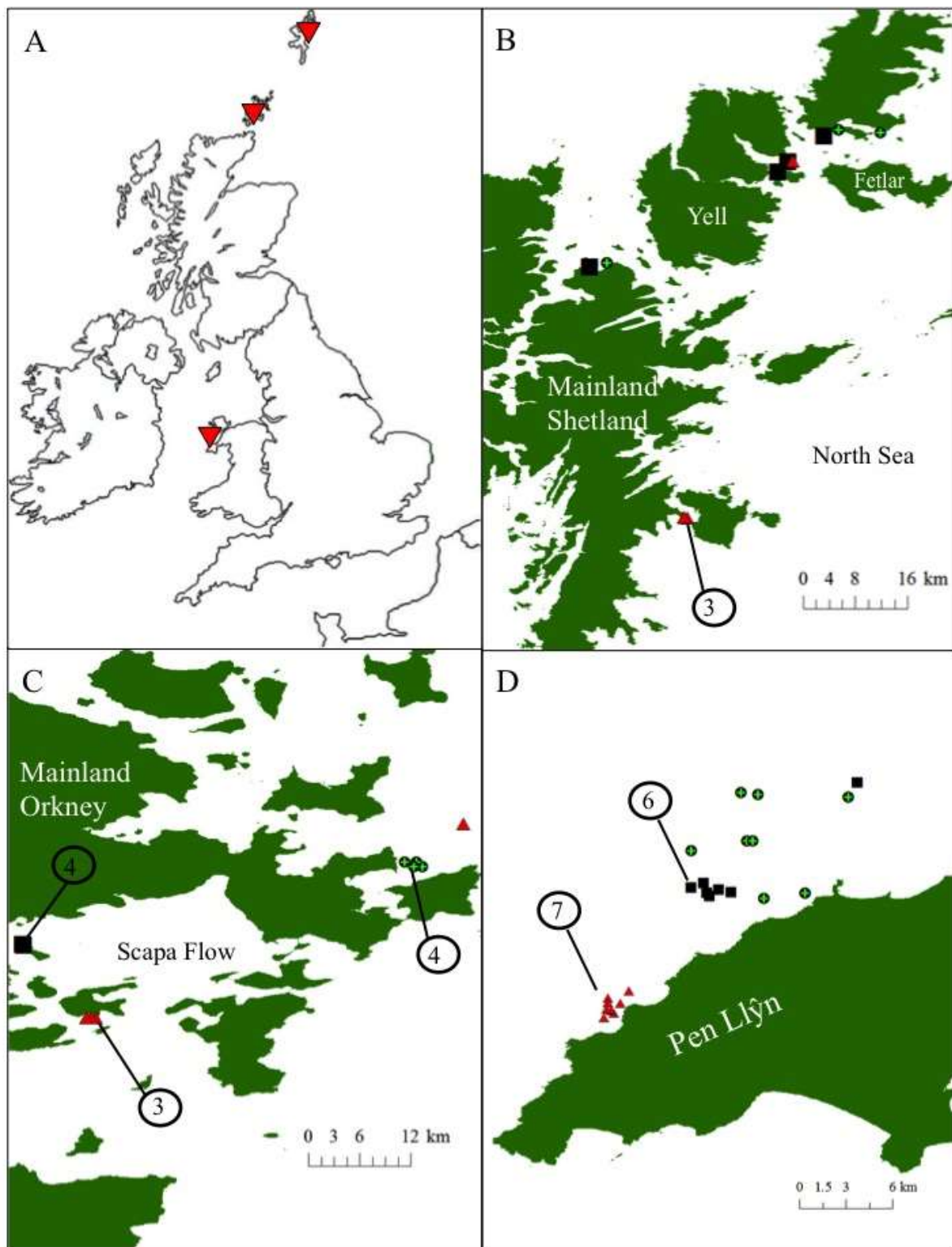
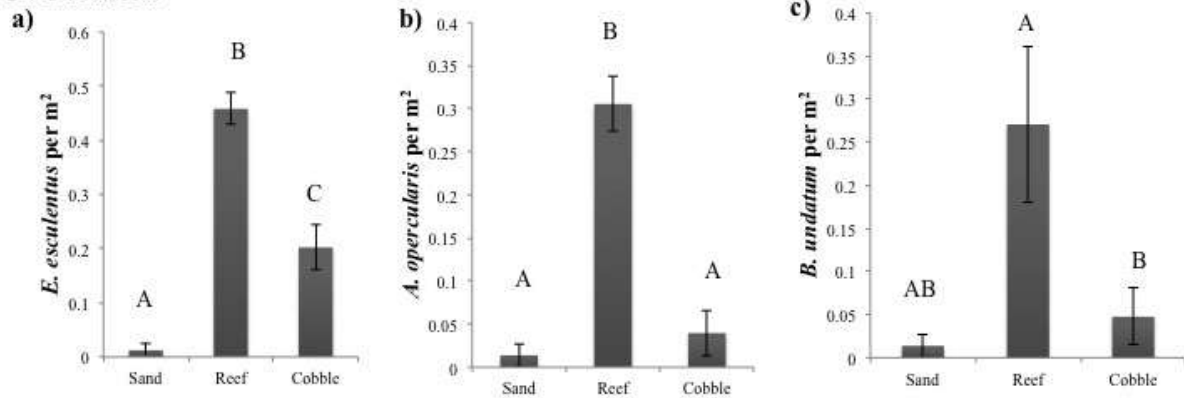


Figure 1. A) *M. modiolus* reefs study regions for megafauna abundance within the UK. B) Survey locations in Shetland (UVC method); C) Orkney (UVC method and stable isotope samples collected); and D) Pen Llŷn (Drop Down Video method). Positions are labelled with the number of sites where markers overlap. Black circle with green cross = sand habitats (16 sites in total); solid square = *M. modiolus* reefs (15 sites in total); red triangle = cobble habitats (15 sites in total).



Figure 2. A) UVC transect technique, B) *Aequipecten opercularis*, C) *Pholis gunnelus*, D) *Buccinum undatum*, E) *Echinus esculentus* and *Asterias rubens* and F) *Pomatoschistus pictus*. Images A, B, D, and E: Richard Shucksmith, images C and F: George Stoye.

UVC transects



DDV transects

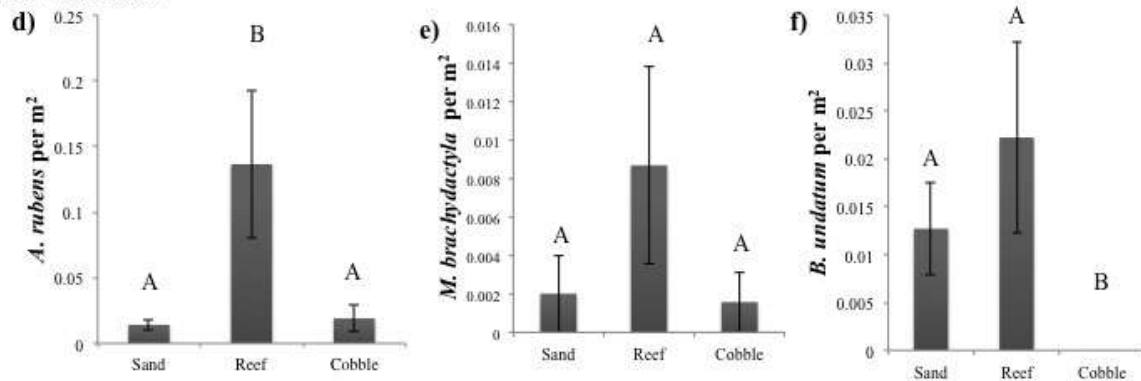


Figure 3. Counts of the key megafauna species from the UVC transects a) b) and c) and the DDV transects d), e) and f). Bars show the mean \pm 1SE. Groups that share a capital letter are not significantly different at the 0.017 probability threshold (Bonferroni correction on Kruskal Wallis test).

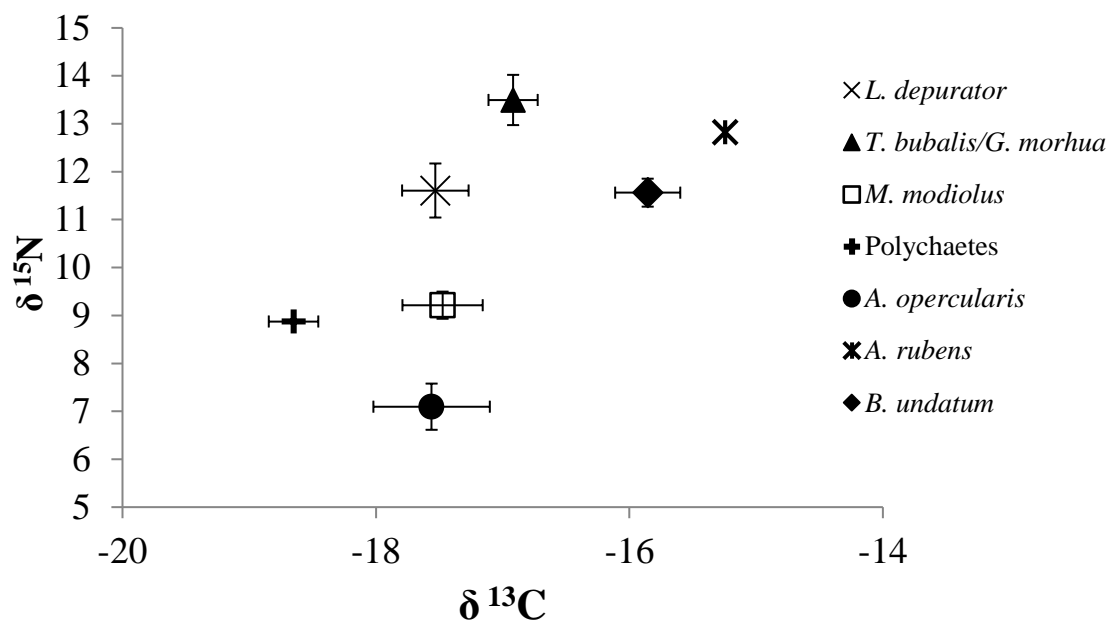


Figure 4. Carbon and Nitrogen isotope biplot of the *M. modiolus* reef community in Scapa Flow, Orkney showing average values \pm 1 SD.

Supplementary information

S1. Location of dive sites for stable isotope sample collection in Orkney

Site	Latitude		Longitude	
West Cava	58	52.718	3	11.458
East Cava	58	50.966	3	11.041
Karlsrhue 1	58	53.357	3	11.394

S2. Underwater Visual Census (UVC) key species pairwise comparisons (Kruskal Wallis tests), Bonferroni correction; significance at $p < 0.016$.

Key Species	Habitat comparison	X ²	P value
<i>Buccinum undatum</i>	Reef & Cobble	3.84	0.0500
	Reef & Sand	7.1358	0.0076
	Cobble and Sand	0.686	0.4073
<i>Aequipecten opercularis</i>	Reef & Cobble	11.0112	0.0009
	Cobble & Sand	0.6868	0.4073
	Reef & Sand	12.4272	0.0004
<i>Echinus esculentus</i>	Reef & Cobble	9.422	0.0021
	Cobble & Sand	10.8482	0.0009
	Reef & Sand	12.3077	0.0005

Drop Down
Video (DDV)

585 key species pairwise comparisons (Kruskal Wallis tests), Bonferroni correction; significance at $p <$
 586 0.016.

587

Key Species	Habitat comparison	X ²	P value
<i>Buccinum undatum</i>	Reef & Cobble	6.55	0.0100
	Reef & Sand	0.0269	0.8690
	Cobble & Sand	6.5502	0.0100
<i>Maja brachydactyla</i>	Reef & Cobble	2.6042	0.1066
	Reef & Sand	2.6042	0.1066
	Cobble & Sand	0	1.0000
<i>Asterias rubens</i>	Reef & Cobble	9.258	0.0023
	Cobble & Sand	0.0509	0.8214
	Reef & Sand	11.618	0.0007

588